Factors that Influence Tunneling in the Eastern Subterranean Termite, *Reticulitermes flavipes* (Kollar) (Isoptera: Rhinotermitidae)[1]

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ABSTRACT Although subterranean termite (Isoptera: Rhinotermitidae) foraging behavior involves the construction of gallery systems in soil, few studies have examined how colony size or soil environmental factors influence rates of construction and morphology of gallery systems. In this study, we investigated the effects of soil texture, soil moisture, and termite density on the rate of tunnel construction and tunnel morphology in *Reticulitermes flavipes* (Kollar). Tunneling rate and tunnel morphology were measured in laboratory arenas by simulating a thin slice of subterranean habitat. Tunneling rates were faster in arenas containing soils with higher sand concentrations. High termite densities had little effect on tunneling rates in small gallery systems, but differences were observed after gallery systems became large. The rate of tunnel construction along edges of tunneling arenas was significantly greater than in the interior. Tunneling distance on days after the addition of water was higher than on days prior to adding water. Differences in tunnel morphology were variable and were not associated with treatment levels in any of these experiments. The results of this study suggest that *R. flavipes* tunneling rates are strongly influenced by environment, whereas tunnel morphology is variable but not associated with any of the factors we examined. Key environmental variables include soil texture, moisture availability, and tactile orienting stimuli.

KEY WORDS Isoptera, Rhinotermitidae, *Reticulitermes flavipes*, subterranean termites, foraging, tunneling, gallery system, tunneling rate, tunnel morphology, orienting stimuli

Resource acquisition and colony survival in subterranean termites depends on the construction of a series of tunnels, or galleries, within a three-dimensional soil matrix (Grace 1992). The majority of subterranean termite gallery systems are near the soil surface (Lee & Wood 1971), but galleries also are constructed several meters below the surface (Watson 1960) and may extend laterally over a thousand square meter area (Grace et al. 1989, Grace 1990, Su et al. 1993). Because of the extent of these gallery systems, they are likely to be as important, although a less conspicuous feature of soil ecosystems as the mounds of mound-building termites

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(Lee & Wood 1971). Construction of a gallery system brings a termite colony into contact with food resources (Ettershank et al. 1980). Gallery systems are, therefore, a record of the foraging activities of subterranean termites.

Gallery construction by subterranean termite colonies may be influenced to some degree by behavioral phenotypes that maximize foraging efficiency. Proponents of optimal-foraging theory assert that foraging movements are, in part, a consequence of natural selection promoting behavioral phenotypes that maximize foraging efficiency (Pyke et al. 1977, Pyke 1978, Krebs & Davies 1991). Foraging efficiency may be an important selective mechanism for subterranean termites because gallery construction is labor intensive compared with insects that travel aboveground (Vleck, 1979). When energy is limited, unproductive movements are detrimental and the selection of more efficient gallery construction behaviors within the population may result.

Recent studies have identified gallery construction behaviors that may affect foraging efficiency in subterranean termites. Robson et al. (1995) demonstrated how the geometry of search tunnel construction in laboratory arenas occupied by *Reticulitermes flavipes* (Kollar) minimized the overlap of the area being searched. Subterranean termites in these experiments divided the total search area equally as a function of the number of galleries produced. In *Coptotermes formosanus* Shiraki, Hedlund & Henderson (1999) showed that primary tunnels were always longer than secondary or tertiary tunnels, and stated that this may be an important component of searching for resources in distant areas. Puche & Su (2001) showed that termite gallery systems display a fractal dimension (Mandelbrot 1983), or pattern of self-similarity at different spatial scales.

Although behavioral phenotypes may be important, there is also evidence that extrinsic environmental factors can influence gallery system construction by subterranean termites. Reinhard et al. (1997) demonstrated that the subterranean termite *Reticulitermes santonensis* De Feytaud detected volatiles emanating from a food source and oriented tunneling activities toward that source. Ettershank et al. (1980) provided strong evidence that subterranean termites are able to detect "thermal shadows" from objects located at the soil surface. They concluded that temperature gradients below surface objects provide a mechanism for directed search and location of food resources. Delaplane & LaFage (1989) postulated that depleted food resources provide a stimulus for tunnel construction and experiments by Hedlund & Henderson (1999) demonstrated that gallery systems in experimental arenas containing small amounts of wood were significantly longer than tunnel networks in arenas with larger amounts of wood. Using laboratory assays, Forschler (1994) and Kuriachan & Gold (1998) found that subterranean termites were able to locate gaps of untreated soil within termiticide-treated barriers, thus demonstrating an adaptive response to soil environmental conditions.

The objectives of this study were to examine the influence of termite density, soil texture, and moisture availability on subterranean termite gallery system construction. Specifically, we looked at the influence of these factors on variables associated with tunneling rate and tunnel morphology, including daily tunneling distance, tunnel branching angle, and distance between tunnel branches. We also compared tunneling rates in open soil to tunneling rates along edges to understand the influence of tactile orienting stimuli in the soil environment.

Materials and Methods

Laboratory tunneling arenas (Fig. 1) were constructed using two sheets (50 cm × 50 cm × 2 mm) and four strips (50 cm × 2 cm × 2 mm) of glass. The strips of glass were placed around the perimeter of one glass sheet, overlapping at the corners, and the second sheet of glass was placed on top, creating an interior space approximately 2- to 3-mm thick between the glass sheets. Twelve large binder clips placed around the edges held the glass sheets together. One of the glass sheets had a small hole (approx. 4 mm diameter) drilled through the center (Fig. 1). This hole provided access for termites to enter the interior space of the tunneling arena. The interior space was filled with soil to represent a thin layer of subterranean habitat and the thickness was designed to allow tunneling in two dimensions only.

Soil was analyzed before the experiment by using gas chromatography to ensure that no insecticide residues were present. Soil was poured through 850-μm sieves (U.S. Standard Sieves, W. S. Tyler Co., Cleveland, Ohio) prior to being used in the tunneling arenas to eliminate larger aggregates and pebbles, thus creating a soil with a uniform texture. After passing through the sieves, all soil particles placed in tunneling arenas were less than 0.850 mm in diameter.

After covering the termite access hole with a piece of tape, individual chambers were turned upright and the glass strip along the top edge was removed. A mailing envelope with both ends cut off was inserted into the top of the chamber

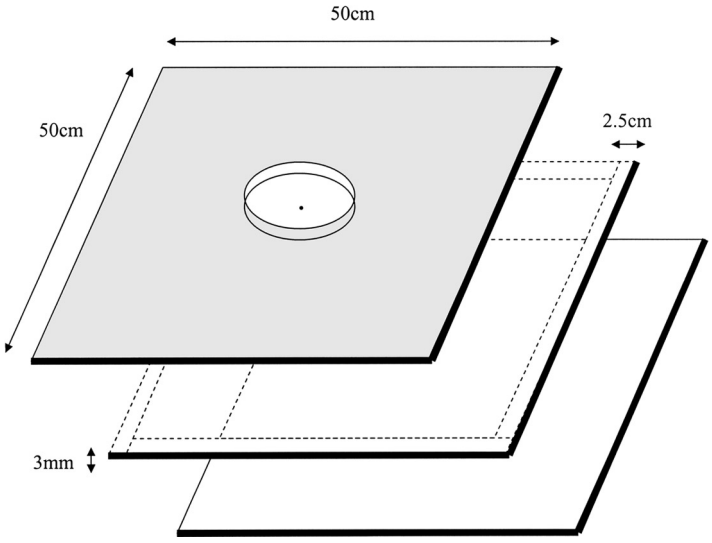

Fig. 1. Expanded view of laboratory arenas used to record tunneling movements of *Reticulitermes flavipes*. The top sheet of glass had a single hole in the center, whereas the lower sheet did not. Four strips of glass were placed around the edges to create a hollow interior that was filled with soil. A Petri dish with a hole in the bottom was placed over the hole in the top glass sheet. The edges were secured with metal binder clips.

to serve as a thin funnel. Arenas were filled by pouring approximately 850 ml of soil through the modified envelope into the interior space of the tunneling arena. Gentle tapping of the glass while pouring the soil helped established a uniform soil density. When interior spaces were filled with soil to a distance of approximately 2 cm from the top, the glass strip was placed back into the space along the top edge and clamped in place. Caution was taken to ensure that no empty spaces existed which would allow the soil to shift inside the arenas.

Soil-filled tunneling arenas were laid flat and the tape was removed from the access hole. A large, circular, polystyrene Petri dish, 14 cm in diameter by 2.5 cm tall (Becton Dickinson & Co. Labware, Lincoln Park, New Jersey), with a small hole in the bottom was attached with silicone glue to the tunneling arena. The hole in the bottom of the Petri dish was aligned with the entrance hole in the glass sheet. Moistened, wooden tongue depressors, weighing approximately 19.5 g, were placed in the Petri dish to serve as a food source.

Tunneling arenas were placed on wire racks inside environmentally controlled, walk-in growth chambers. Temperature and humidity were controlled at 25 ± 1°C and 70 ± 2%RH within environmental chambers. Wire racks consisted of four wire shelves stacked above one another. Each wire shelf was approximately 2 m in length and was able to accommodate four tunneling arenas placed side by side. Four small lengths of PVC pipe (approx. 10 cm) were cut and laid on their ends to support each tunneling arena. The vertical distance between shelves was large enough to allow easy observation of the top and bottom of each arena. A plexiglass sheet was placed above the top shelf to minimize the desiccating effects of air movement from cooling fans in the ceiling.

Sixteen experimental units could be placed within each environmental chamber. Four replications of four treatment levels of soil texture, termite density, and source colony were compared for differences in tunnel rate and tunnel morphology using a randomized complete block design. Treatments and replications were blocked according to shelf (bottom, middle–bottom, middle–top, top) and position on the shelf (left, middle–left, middle–right, right).

Reticulitermes flavipes pseudergates were placed in the center dish with the food source and allowed to tunnel until their tunnels reached and completely encircled the outer edge of the foraging arena. All *R. flavipes* pseudergates were collected from the same bucket trap (Tamashiro et al. 1973, Su and Scheffrahn 1986) in Longmire Park, College Station, Texas, within the same week and held in the laboratory for less than a month before being placed into tunneling arenas. The large number of termites that needed to be collected within these time parameters precluded the use of more than one colony in these experiments. However, preliminary experiments (Houseman-unpublished data) at selected soil textures and termite densities showed that *R. flavipes* colonies from Longmire Park, Lemon Tree Park and Texas A&M-Trailer responded similarly in terms of tunneling rate and tunnel morphology to conditions within tunneling arenas.

At 24-h intervals after termites were introduced, tunneling arenas were examined and the terminal ends of all tunnels were marked on the glass using a fine point Sharpie® permanent marker (Sanford, Bellwood, Illinois). Four different colors of marker were used alternatively on consecutive days throughout the experiment. The number of days since introducing termites was written beside each mark. No tunnels were marked until they extended out from under the Petri dish. This initial period allowed the termites to become acclimated to the tunnel-

ing arena. Water was added to the Petri dish at 3- to 4-day intervals to help maintain suitable moisture levels within foraging arenas. Observations were made and marks recorded at the end of each 24-h period, until tunnels reached and completely encircled the outer edge of the foraging arena.

After tunneling was complete, all tunnels were traced directly onto the glass sheet using a black Sharpie® permanent marker (Sanford, Bellwood, Illinois). A lamp placed under the tunneling arena highlighted tunnels and increased the accuracy of tracing. Small, triangular, adhesive markers were placed along the length of the traced tunnel at the exact locations of the colored marks representing each 24-h period (Fig. 2). The number of days since introducing termites was written on each adhesive marker.

After tracing and marking tunnels, foraging arenas were completely disassembled. Glass sheets containing traced images were placed on a photocopy machine and the tunnel images copied to paper. The copies were then digitized using a flatbed scanner. Daily tunneling distances, branching angles, and distances between branches were measured (Fig. 2) from digitized tunnel images using SigmaScan® Pro 5.0 (SPSS, Chicago, Illinois). Tunneling rates were calculated by dividing the total distance tunneled by the total number of days. Branching angles were measured as the straight-line angular deviation between divergent tunnels at 1cm distance from the branch point. Studies by Robson et al. (1995) showed that angular measurements taken at this distance were significantly

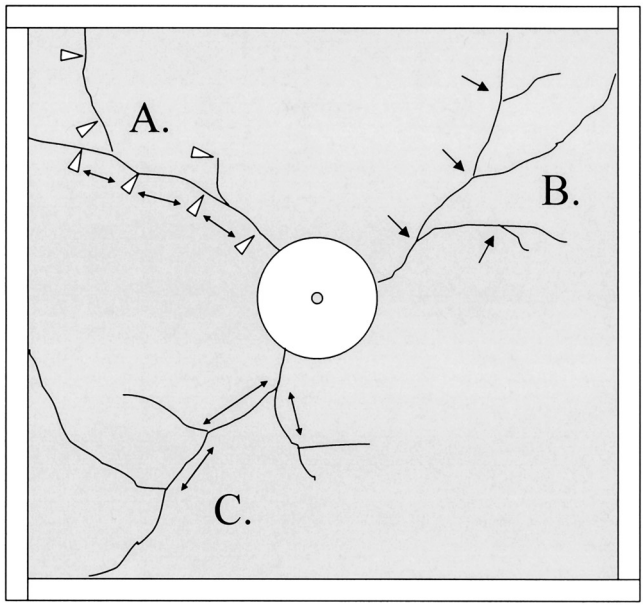

Fig. 2. Tunnel characteristics measured for each experimental tunneling arena after introducing *Reticulitermes flavipes*. Daily tunneling distance (A), tunnel branching angle (B), and distance between tunnel branches (C) were quantified to determine differences in tunneling rate and tunnel morphology between treatments.

correlated with angles measured at distances of 5, 10, and 20 cm along divergent tunnels.

Kruskal–Wallis analysis of variance was used to examine treatment effects ($\alpha = 0.05$) on tunneling rate and tunnel morphology. Pairwise comparisons between treatments were conducted using Tukey's Test ($\alpha = 0.05$). Interior tunneling rates were compared with edge tunneling rates within treatment levels using a Paired *t* test ($\alpha = 0.05$).

Soil texture. Four treatments were prepared using mixtures of pure sand (TXI Inc., Houston, Texas) and natural soil from College Station, Texas. Pure soil, pure sand, 2:1 soil to sand, and 2:1 sand to soil mixtures were compared. Ratios of sand and soil were based on volume. Textural analysis for each treatment gave the exact proportions of sand, silt, and clay (Table 1). These proportions correspond to sandy, loamy-sand, sandy-loam and loamy soil textures. These textures are referred to hereafter by the proportion of sand in the mixture (i.e., pure soil = 31% sand, 2:1 soil to sand = 58% sand, 2:1 sand to soil = 80% sand, and pure sand = 100% sand). Four repetitions from each textural class were used.

Two-thousand *R. flavipes* pseudergates were introduced into each tunneling arena (4 treatments × 4 replicates × 2,000 = 32,000 termites). Approximately 10 ml of water were added at 3 to 4 d intervals until the last tunneling arena finished.

Termite density. Treatment levels of 500, 1,000, 2,000 and 4,000 pseudergates per tunneling arena were examined. Four replications were performed at each termite density (4 replications × 500 + 4 replications × 1,000 + 4 replications × 2,000 + 4 replications × 4,000 = 30,000 termites). Because the internal dimensions of the tunneling arena were equal to 0.25 m^2, actual numbers of termites can be converted to densities of 2,000, 4,000, 8,000 and 16,000 termites per m^2.

An 80% sand mixture was used to test all levels of population size. Approximately 5 ml distilled water was added to central dishes at 3 d intervals until the last arena was finished.

Moisture effects. Because different amounts of water were added in soil texture (10 ml) and termite density (5 ml) experiments, tunneling data from treatments containing 80% sand and 2000 termites were compared to examine the effects of moisture availability on termite tunneling rates. Mean tunneling rates per gallery on the day before and the day after adding 5 or 10 ml of water were compared using a Paired *t* test ($\alpha = 0.05$). Comparisons were made for both the interior and along edges.

Table 1. Percent sand, silt, and clay for each of four soils used to evaluate the influence of soil texture on *Reticulitermes flavipes* tunneling rate and tunnel morphology.

Treatment	Sand %	Silt %	Clay %
A	31	54	15
B	58	33	9
C	80	16	4
D	100	0	0

A, soil alone; B, 2:1 soil/sand mixture, C, 2:1 sand/soil mixture; D, sand alone.

Results

Analysis of variance revealed significant differences ($\alpha = 0.05$) between the number of days to reach and encircle the edge for different soil textures and termite densities (Table 2). Significant differences ($\alpha = 0.05$) were found between interior tunneling rates for different soil textures (Table 2) and between edge tunneling rates for different soil textures and termite densities (Table 2). Significant differences ($\alpha = 0.05$) in tunneling rate were also found between the interior and along edges (Table 3) and between days before and after adding water (Table 4).

Mean branching angles were highly variable, ranging from 48.7 to 73.9 degrees in all soil textures and densities (Table 2). Distances between tunnel branches also varied widely and ranged from 2.8 cm to 9.1 cm (Table 2). No significant differences ($\alpha = 0.05$) between branching angles or distances between branches among treatment levels of soil texture or termite density were identified.

Soil texture. The mean numbers of days to reach and encircle the outer edge of tunneling arenas were 10.33, 16.75, 23.0, and 30.0 days (Table 2). Pairwise comparisons showed that 31%, 58%, 80%, and 100% sand were all significantly different ($\alpha = 0.05$) from one another (Table 2).

Interior tunneling rates were 4.48, 6.19, 10.1, and 12.12 cm/day (Table 2). Pairwise comparisons ($\alpha = 0.05$) showed that pure sand was different from pure soil. Tunneling rates along edges were 12.67, 18.65, 26.66, and 42.06 cm/day (Table 2). Pairwise comparisons revealed that tunneling rates along edges in 100% sand were significantly higher ($\alpha = 0.05$) than 31% and 58% sand (Table 2).

Termite density. The mean numbers of days to reach and go completely around the edge were 17.25, 22.0, 24.75, and 29.25 days (Table 2). Pairwise comparisons showed that 500 termites took significantly ($\alpha = 0.05$) longer than 2,000 or 4,000 termites to finish the assay (Table 2).

Mean interior tunneling rates were 8.38, 11.16, 11.86, and 11.98 cm/day (Table 2). Interior tunneling rates at different densities were not significantly different ($\alpha = 0.05$) from one another. Mean edge tunneling rates were 13.67, 17.62, 19.34, and 22.32 cm/day (Table 2). The tunneling rate of 4,000 termites was significantly ($\alpha = 0.05$) higher than 500 or 1,000 termites, but not 2,000 (Table 2).

Interior versus edge. Tunneling rates ranged from 1.6 to 3.5 times higher along edges than in the interior at all soil textures and termite densities (Table 3). Paired t tests revealed that tunneling rates were significantly higher ($\alpha = 0.05$) along edges for all soil textures and all termite densities except 1,000 termites (Table 3). However, differences in this treatment were still very nearly significant ($P = 0.06$).

Moisture effects. In experiments where 5 ml of water was added, Paired t tests showed that tunneling rates on the day after water was added were significantly greater ($\alpha = 0.05$) than the day before adding water (Table 4). In experiments where 10 ml of water were added, the mean distance tunneled on the day after water was not significantly different ($\alpha = 0.05$) from the day before adding water (Table 4).

Discussion

Soil texture. The influence of soil texture on tunneling rate was related to sand concentration and may be explained by the size of particles removed during

Table 2. Summary of mean values measured for *Reticulitermes flavipes* tunneling rate and tunnel morphology in tunneling arenas containing different soil textures and termite densities.

Experiment	Treatment	Mean finishing time (days)[a]	Mean interior tunneling rate (cm/day)[a]	Mean edge tunneling rate (cm/day)[a]	Mean branching angle (degrees)[a]	Mean internode distance (cm)[a]
Soil texture	31% sand	30.0 a	4.48 a	12.67 a	60.25 a	3.80 a
	58% sand	23.0 b	6.19 ab	18.65 a	61.53 a	9.10 a
	80% sand	16.75 c	10.1 ab	26.66 ab	73.88 a	7.80 a
	100% sand	10.33 d	12.12 b	42.06 b	56.07 a	6.00 a
	Kruskal–Wallis	$F = 30.83$	$F = 3.62$	$F = 7.95$	$F = 1.36$	$F = 1.61$
		$P = 0.001$*	$P = 0.049$*	$P = 0.004$*	$P = 0.32$	$P = 0.26$
Termite density	500 termites	29.25 a	8.38 a	13.67 a	57.88 a	5.60 a
	1000 termites	24.75 ab	11.16 a	17.62 ab	59.45 a	2.80 a
	2000 termites	22.0 bc	11.98 a	19.34 bc	57.60 a	3.98 a
	4000 termites	17.25 c	11.86 a	22.32 c	54.58 a	4.43 a
	Kruskal–Wallis	$F = 11.41$	$F = 0.871$	$F = 11.22$	$F = 0.94$	$F = 0.76$
		$P = 0.001$*	$P = 0.48$	$P = 0.001$*	$P = 0.45$	$P = 0.58$

Significant overall differences according to Kruskal–Wallis ANOVA ($\alpha = 0.05$) are annotated with an asterisk (*).

[a]Significant pair-wise differences between means within columns according to Tukey's Test ($\alpha = 0.05$) are indicated by different letters.

Table 3. Summary of mean values for *Reticulitermes flavipes* tunneling rates (cm/day) measured in the interior and along edges of tunneling arenas containing different soil textures and termite densities.

		Mean tunneling rate (cm/day)			
Experiment	Treatment	Interior	Edge	*t*	*P*
Soil texture	31% sand	4.48	12.67	–4.822	0.003*
	58% sand	6.19	18.65	–5.260	0.002*
	80% sand	10.1	26.66	–3.012	0.02*
	100% sand	12.12	42.06	–3.567	0.02*
Termite density	500 termites	8.38	13.67	–7.084	0.001*
	1000 termites	11.16	17.62	–2.309	0.06
	2000 termites	11.98	19.34	–3.581	0.01*
	4000 termites	11.86	22.32	–4.666	0.003*

Significant differences ($\alpha = 0.05$) are annotated with an asterisk (*).

each visit in sand versus soil. Sand particles are larger than other soil particles and as the size of the individual particles increases the number of particles in a given space decreases. Thus, tunneling in 100% sand would minimize the number of soil particles needing to be removed. In addition, the amount of space created each time a termite removes a sand particle is also greater than when other soil particles are removed, which reduces the number of visits needed to extend the tunnel.

Large soil particles do not fit as close together as smaller soil particles, so larger interstitial spaces exist between sand grains than between other soil particles. The total amount of this 'empty' space is maximized in tunneling arenas filled with 100% sand. Even when a small proportion of smaller silt and clay particles are mixed with sand, these smaller particles can fill the interstitial

Table 4. Summary of mean values for *Reticulitermes flavipes* tunneling rates (cm/day), measured 24 h before and 24 h after water was added to the central dish in arenas containing 80% sand and 2000 termites.

		Mean tunneling rate (cm/day)			
Location of tunnel	Water	24 h before	24 h after	*t*	*P*
Interior	5 ml	7.27	17.07	3.43	0.014*
	10 ml	7.81	13.75	1.22	0.270
Edge	5 ml	11.48	29.72	3.16	0.020*
	10 ml	18.59	26.79	1.47	0.191

Significant differences ($\alpha = 0.05$) are annotated with an asterisk (*).

spaces between sand grains and significantly reduce the amount of empty space. Less empty space means more soil must be moved, which requires more visits and reduces tunneling rate.

Termite density. The moderate effect of termite density on tunneling rates in this experiment is surprising since it seems reasonable to hypothesize that as the number of available workers increases there would be an increase in the number of round trips that could be made to move soil particles during a given period of time. However, it is possible that these effects could be offset by other density-dependent factors that restrict tunneling of larger groups compared with smaller groups.

Because gallery systems have a finite amount of available space for termites to occupy, the amount of space within galleries may place constraints on the soil-moving activities of large groups relative to small groups. In this experiment, tunnel systems were started *de novo*, with no available tunnel area initially, and increased daily as tunnels were constructed. In small gallery systems, larger termite populations have a higher proportion of individuals that are not able to enter the gallery system because of space constraints. Because the amount of "excess" termites presumably has little effect on overall tunneling rate, space constraints may reduce the advantages of large termite groups when compared with small groups.

By necessity, interior tunneling rates were measured in this experiment when gallery systems were smallest and space constraints were likely present. Edge tunneling rates, however, could only be measured after gallery systems were larger. Therefore, space constraints could explain why interior tunneling rates were similar, whereas differences in tunneling rate were measured for different densities only after gallery systems were large enough to reach the edge of tunneling arenas.

Interior versus edge. Subterranean termites tunneled at higher rates along the edges of tunneling arenas. Tunneling rates along edges were approximately twice as large as interior tunneling rates. Additionally, when tunnels reached the edge of arenas, we observed that termites continued to follow this stimulus instead of branching or turning back toward the center of the arena. These observations demonstrate that *R. flavipes* responds to tactile stimuli during tunneling, and may indicate the importance of edge stimuli in the subterranean environment. Common edge stimuli in the subterranean environment include the boundaries of roots, rocks, pipes, cables, or other structures.

Subterranean termite pseudergates in the genus *Reticulitermes* live in a dark soil environment and do not have visual receptors so they must rely on chemical and tactile orienting stimuli in their environment (Grasse 1945, Barth 1955, Stuart 1964). Pseudergates have various bristles, pores, and diffuse nerve endings used to sense their surroundings, but trichodea sensilla are presumed to function in tactile perception of the environment (Richard 1969). Although trichodea sensilla are distributed over the entire body, Richard (1969) noted that they are more concentrated on the head and legs. These are also the areas of the body that are used for moving soil.

There could be a selective advantage associated with responding to tactile stimuli provided by edges in the subterranean environment. In nature, interstitial spaces may be associated with edges in the soil matrix. Because tunneling is labor intensive, movement of *R. flavipes* within interstitial spaces along edges

would reduce the amount of energy expended to create a gallery system in the subterranean environment. This increase in tunneling efficiency may provide a selective advantage for behavioral phenotypes that respond to and follow edge stimuli.

It is also possible that the behavioral response by *R. flavipes* to edges in the soil environment could include more than simply following the stimulus or taking advantage of interstitial spaces. The response may be more complex and could include recruitment of nestmates to the stimulus. In these experiments there were no interstitial spaces along edges to explain dramatic increases in tunneling rate, however, recruitment of additional nestmates to edge stimuli could account for observed differences in tunneling rate. Although not quantified, there appeared to be higher numbers of termites at the termini of tunnels along edges than at the termini of interior tunnels. Higher numbers of termites working along edges would increase the number of soil particles removed and result in increased tunneling rates relative to the interior. It would be useful to further investigate the behavioral responses of *R. flavipes* to edge stimuli in their environment to determine whether recruitment is occurring.

Moisture effects. When 5 ml of water were added to foraging arenas the effects of dessiccation resulted in reduced tunneling rates after 1–2 d. However, when 10 ml of water were added, there was sufficient moisture to maintain more similar tunneling rates. Moisture effects in this study support observations by Collins (1958) and Collins & Richards (1963), who showed that *R. flavipes* is sensitive to low moisture levels and responds to desiccation by moving toward areas of favorable soil moisture. In treatments where smaller amounts of moisture were added, termites may have responded by staying nearer to the central dish. This behavioral response would minimize the number of termites visiting tunnel termini and reduced tunneling rates would result.

These results are also consistent with reports that *R. flavipes* activity in natural landscapes is related to soil moisture (Houseman et al. 2001). Because seasonal and spatial distribution of soil moisture varies in natural landscapes, this variation could affect both the location and timing of tunneling activity. Based on these tunneling experiments, we might predict that gallery system construction by *R. flavipes* would be reduced during dry seasons. As a result of reduced tunnel construction, the discovery of new food resources may also decrease during drier periods. We might also predict that tunneling activities in landscapes would spatially correspond with areas of favorable soil moisture, while areas of low soil moisture would function as filters of termite movement within the landscape.

The results of this study suggest that *R. flavipes* tunneling behavior is strongly influenced by certain key factors in the soil environment. Differences in tunneling rate between soils of different textures is due to the size and number of soil particles that need to be moved, and does not seem to be the result of a differential behavioral response by *R. flavipes*. In contrast, moisture availability and tactile orienting stimuli may elicit important behavioral responses in *R. flavipes* that can influence the rate of tunnel construction in soil environments.

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